NOTES ON SPATIAL DISTRIBUTION PATTERNS

FOR THREE MEXICAN SPECIES OF BEGONIA*

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ABSTRACT

Nine 25 x 30 meter quadrats were plotted for three species of Begonia at several locations in Mexico in order to determine spatial distribution patterns. These data only superficially describe the patterning for these species. The three species observed were Begonia californica, Brand., B. heracleifolia, Schlechtd. and B. nelumbiifolia Schlechtd. and Cham., the latter two being observed to occur sympatrically in one area of Chiapas. Spatial patterns were analyzed according to abundance (A), frequency (F), density (D), and A/F ratio, clumping behavior, common boundary values (CBV), and sympatric association. B. heracleifolia is found to have the lowest values for A, D, and F, B. californica the next, and B. nelumbiifolia the highest values, though the order is reversed respectively for A/F ratio with B. heracleifolia being the highest and B. nelumbiifolia the lowest. An analysis of clumping behavior indicates that as the values of A, D, F, or A/F increase there is a general increase in the number of individuals occupied in clumps and correspondingly a lower percentage of individuals occurring singly. CBVs indicate that B. heracleifolia has the greatest tendency for contiguous distribution within regional populations in spite of its low A, D and F values and lower number of individuals/quadrat. Distinct patterns of dominance are exhibited by B. heracleifolia and B. nelumbiifolia even though they occur sympatrically within the same quadrat; it is found that 55% of the classifiable groups are comprised of a single species, 30% show a minimum of 75% dominance by one species, and the remaining 15% have between 63% and 66.7% dominance. Distinct habitat preferences are revealed by the sympatry of B. heracleifolia and B. nelumbiifolia around the base of the waterfall where the quadrats were set up; the former species occupies areas closer to the edge of the surrounding forest and the latter being found more frequently near the margin of the pool. No hybridization was observed between these two species.

INTRODUCTION

While on collecting expeditions in Mexico during several months of 1975 and 1976, I made casual observations on the spatial distribution patterns of three species of Begonia. This paper is limited in data and thus makes no attempt to provide a complete description of the spatial patterning for the three species, but is a systematic approach to the observations made.

The recent applications of spatial distribution patterns among plant groups are varied, and several have involved work in tropical environments. Fedorov (1966) concluded that tropical tree families, often represented by many species, frequently occur in low densities and the individuals within a given regional population often are isolated from each other, even in cases where the species was very abundant. Contrary to Federov's work are the results of Poore (1968), who points out that contiguous distribution of individuals is common among certain rainforest tree taxa. Ashton (1969) reports on spatial distribution patterns and speciation among tropical forest trees in West Sarawak, Borneo, with particular references to species in the Apocynaceae, Dipterocarpaceae, Moraceae, and Sapotaceae. Working in Costa Rica, Bawa and Opler (1977) report on the spatial patterning of staminate and pistillate taxa within the Meliaceae, Rubiaceae, and Polygonaceae. Also working in tropical lowland rainforest of Costa Rica were Richards and Williamson (1975) who report on the patterns of understory species following large treefalls. Though not specifically dealing with spatial distribution, there is a study by Smith (1975) on the distribution of herbaceous angiosperm species in the mountains of New Guinea. A number of distribution pattern studies have been carried out among north temperate climate plants. Day and Monk (1974) analyzed an Appalachian watershed community in terms of several topographic parameters. Distribution patterns of two species of Artemisia were studied in relation to certain environmental factors including soil preferences, ion exchange variances, and distribution of other plant species (Hazlett and Hoffman, 1975). Two evolutionary studies utilizing distribution patterns were conducted on the Cruciferae: Solbrig and Rollins (1977) mention distribution patterns in their investigations on the autogamy of Leavenworthia and the patterning of Pierid butterfly eggs on various Southern Rocky Mountain cruciferous plants has been carried out by the Chews (1977). The distribution patterns of Thymelaea hirsuta (L.) Endl. and its associated flora was analyzed along the Mediterranean coast of Egypt by El-Ghonemy et al. (1977).

The Begoniaceae is a small family characterized by the genus Begonia, which has approximately 1600 species (Barkley and Golding 1972), though new species are being discovered with additional exploration. The Begoniaceae are found geographically in the tropics worldwide and in some semi-tropical areas. Field observations on

my part from countries in the neotropics and old world tropics in-
dicate that Begonia has a preference for stream margin habitats,
though other habitats are encountered. Regal (1977) points out
that the unstable stream margin habitat of the tropics is an
ancient ecosystem. Several other characteristics of Begonia are
of botanical interest also: 1) Species of Begonia are monecious.
Observations from growing about 75 species in cultivation indi-
cate that the staminate flowers always appear before the pistil-
late flowers, 2) medullary and cortical vascular bundles are
found in certain taxa of the genus (Debary 1884), 3) a high fre-
quency of polyploidy is present within the genus (Darlington 1955)
and (Legro and Doorenbos 1969, 1971), 4) the presence of residual
meristematic potential of the leaves of many species have the
capability of reproducing new plants (Howard 1974), and 5) the
stomata of many species of Begonia occur in distinct clumps, where
each stoma is separated by subsidiary cells and the clumps them-
selves are separated by epidermal cells (Barkley, personal com-
munication and Hoover, unpublished results).

Clumping behavior was observed for several species of Begonia
in Colombia, of which two occurred sympatrically in close asso-
ciation, B. hexandra Irm. and B. toledana Smith and Schubert
(Hoover 1974). Unlike the investigation of spatial patterning of
tropical rain forest trees, this study involves patterning of
herbaceous plants. Table 1 lists the geographical and regional
locations, elevation, latitude and longitude, and habitat of the
quadrat positions for B. californica, B. heracleifolia and B.
nelumbiifolia. Figure 1 is a map showing these geographical lo-
cations. The latter two species are represented by many collec-
tions in the Gray Herbarium and Missouri Botanical Garden. Review
papers and general studies on the subject of plant spatial distri-
bution are reported in the works by Goodall (1952), Grieg-Smith
(1964), and Kershaw (1964).

METHODS

At this time, the reproductive biology of these species of
Begonia is not known, which does raise questions concerning the
concept of the individual within the quadrats mapped. An indivi-
dual in this study is considered as any separate or distinct or-
ganism, independent of the possibility that it may have been re-
produced vegetatively. Vegetative reproduction, which may fre-
quently occur within Begonia, will result in plants that have
identical genetic systems. The concept of the individual in a
clonal population is an interesting idea and much could be said
about this problem.

A quadrat size of 25M x 30M was chosen as the standard. This
size was adopted from Day and Monk (1974), who chose a 25M x 50M
quadrat for their work in the Appalachians. A smaller quadrat was
found to be practical to work with in the tropics on Begonia, be-
cause the plants of a particular population rarely occupied an area

larger than 750M^2. The 25M x 30M plot size remains constant though the position of individual square meters is an estimation. Great difficulty in maneuvering was frequently encountered. Often the areas to be mapped were littered with slippery logs and boulders, or were very steep, vertical in some locations, due to the habitat conditions where one frequently encounters Begonia. Table 1 indicates that all the quadrats, except No. 6 in Sinaloa, were mapped in stream margin habitats.

The calculations of A, D, and F are referred to by Grieg-Smith (1964) and the ratios for determining them are as follows:

$$A == \frac{\text{Total No. of Individuals}}{\text{Number of Occupied Quadrats}}$$

$$D == \frac{\text{Total No. of Individuals}}{\text{Total No. of Quadrats}}$$

$$F -- \frac{\text{No. of Occupied Quadrats}}{\text{Total No. of Quadrats}}$$

The A/F ratio is determined by the following: $\frac{100D}{F2}$

In the section on CBV, a number of standards were adopted. The groups listed as A, B, C, etc. in Tables 4 and 5, and in Fig. 3 are defined according to a minimum separation of two meters between each group. The CBV is a numerical figure consisting of the number of occupied square meters and the number of common borders shared by clumps within the group. A common boundary is when two or more square meters have an adjacent side or a common point, as with two square meters being diagonal to one another.

Selection of quadrats was largely made according to the availability of the plants. Each quadrat except nos. 1 and 2 represents an isolated population of Begonia in the environment. Quadrats 1 and 2 of B. heracleifolia near Palenque, Chiapas, were randomly selected from an entire section of a stream that was occupied with this species. Except for these quadrats near Palenque, the areas occupied by each of the plots likely represents the bulk of an interbreeding population. At the Misola waterfall in Chiapas a few scattered individuals were observed downstream, but the sympatric population was completely mapped; the cliff face occupied by B. nelumbiifolia was not plotted, for mapping would be extremely difficult and hazardous. In Baja California considerable effort was spent trying to locate B. californica and only at the Las Animas area was this species found. The plots for B. californica were made in November 1976, at which time they were observed as dried up, partially decayed vegetative shoots and capsules. It is unknown how many plants were represented in their tuberous form. In Sinaloa, B. heracleifolia was observed in only one area along the road.

Fig. 1 – Geographical Locations of
         Spatial Distribution Quadrats.

 – Quadrat Locations

TABLE 1

Geographical Locations of Spatial Distributions

for B. californica, B. heracleifolia, B. nelumbifolia

Species	Quadrat Number	Location of Habitat	Elevation	Latitude / Longitude
B. heracleifolia	1	Stream by ruins of Palenque, Chiapas	600-650M	18° / 94°
B. heracleifolia	2	"	600-650M	18° / 94°
B. heracleifolia	3I	Misola waterfall, Chiapas	600-650M	18° / 94°
B. nelumbifolia	3II	"	600-650M	18° / 94°
B. heracleifolia	4I	"	600-650M	18° / 94°
B. heracleifolia	4II	"	600-650M	18° / 94°
B. heracleifolia	5I	"	600-650M	18° / 94°
B. heracleifolia	5II	"	600-650M	18° / 94°
B. heracleifolia	6	Roadside from Mazatlan to Durango, Sinaloa	1500-1700M	23½° / 106°
B. heracleifolia	7	"	1500-1700M	23½° / 106°
B. californica	8	Cerro el Picacho, Baja California Sur	250-350M	23½° / 110°
B. californica	9	"	250-350M	23½° / 110°

It may be important to note that the spatial patterning of these species of Begonia is subject to considerable variation through time. The disturbance of the stream margin habitat of the tropical rainforest is very great and may contribute to understanding the variation within the plant groups occuping these habitats.

ABUNDANCE, DENSITY, AND FREQUENCY ANALYSIS

Table 2 presents the data on the number of individuals in a quadrat, and the A, D, F, and A/F ratios. Quadrat 6 for B. heracleifolia in Sinaloa had the fewest number of individuals of all the plots, where 13 plants were counted. Quadrat 6 correspondingly exhibits the lowest values of A (1.2), D (.017), and F (1.5). The largest number of individuals were found in quadrat 5II for B. nelumbiifolia in Chiapas where 135 plants were counted. Quadrat 5II consists of a sympatric association of B. heracleifolia and B. nelumbiifolia, the latter exceeding the other quadrats in A, D, and F also; these parameters respectively being 4.7, .18 and 4.4. As is expected, the greater the number of individuals in a quadrat, the greater the values of A and D, and generally of F, also, but not for A/F. Due to limited data, the A/F ratio yields little information.

The information in Table 3 is an averaging of A, D, F, and A/F for each species. B. heracleifolia has the lowest average number of individuals per quadrat and the lowest values for A, D, and F, though it has the highest A/F ratio. B. californica ranks second in comparison for the 4 parameters, though it is not much greater among any of them, exceeding B. heracleifolia in number of individuals per quadrat only by 6.1 individuals. As was mentioned above, these figures are less than actual for B. californica because it is not known how many individuals were represented in their tuberous form. B. nelumbiifolia exceeds the other two species in all parameters except A/F ratio which is less than the others, being .85 as compared to .89 for B. heracleifolia, and .87 for B. californica. The higher A/F value for B. heracleifolia may be accounted for by its ability to spread out within the habitat the species has invaded; the higher A/F ratio of this species likely corresponds to its greater CBV.

A noticeable difference in the parameters exists between the quadrats plotted for B. heracleifolia in Sinaloa, nos. 6 and 7, and those in Chiapas, nos. 1, 2, 3I, 4I and 5I; the former are represented by fewer individuals and consequently lower A, D, and F values, as Table 3 shows. Quadrat 7 from Sinaloa does exceed quadrat 3 in total number of individuals, D, and F though not in A or A/F. An F value of 2.8 for quadrat 7 exceeds the F values of all other B. heracleifolia, but averages of the parameters of these northern quadrate are less than those from Chiapas. Several factors may explain why the spatial patterning is different between

TABLE 2

NUMBER OF INDIVIDUALS, A, D, F, AND A/F FOR EACH QUADRAT

Grid No.	Species	Total No. of Individuals	A	D	F	A/F
1	B. heracleifolia	51	3.19	.068	2.13	1.50
2	B. heracleifolia	46	2.56	.061	2.40	1.00
3I	B. heracleifolia	20	1.66	.027	1.60	1.06
3II	B. nelumbifolia	46	2.42	.061	2.53	.95
4I	B. heracleifolia	38	2.38	.051	2.13	1.12
4II	B. nelumbifolia	35	1.75	.047	2.67	.66
5I	B. heracleifolia	51	2.04	.068	3.33	.61
5II	B. nelumbifolia	36	4.00	.181	4.53	.88
6	B. heracleifolia	13	1.18	.017	1.47	.79
7	B. heracleifolia	31	1.48	.041	2.80	.52
8	B. californica	48	2.09	.064	3.07	.68
9	B. californica	36	2.25	.048	2.13	1.06

TABLE 3

MEAN NUMBER OF INDIVIDUALS, AVERAGE A, D, F, AND A/F

Species	Mean Number of Individuals	A	D	F	A/F
B. californica	42	2.2	.056	2.6	.89
B. heracleifolia	35.7	2.11	.048	3.0	.95
Chiapas	.41.2	2.3	.056	2.4	.97
Sinaloa	22	1.4	.029	2.2	.69
B. nelumbifolia	72.3	2.32	.096	3.21	.92

the southern and northern populations. 1. The latitude is much greater than other latitudes where B. heracleifolia has been collected. (There are no other collections from Sinaloa represented in the Gray Herbarium.) 2. The elevation is significantly higher than the average for the section Gireoudia, which is averaged to be 1,050M (Hoover 1976). 3. Environmental factors, particular soil type and moisture availability may not allow for developed clumps. The plants from Chiapas grew on limestone; in Sinaloa plants from quadrat 6 grew in soil and plants from quadrat 7 grew on rocks in a stream bed, quadrat 7 being the more abundant of the two. 4. Competition from other angiosperms. In Chiapas, the dominant herbaceous flowering plants in the quadrats were Begonia. This was not the case in Sinaloa, for the environment in Sinaloa had characteristics that allowed several different species to live successfully. In Chiapas the factors comprising the microhabitat appeared very specific; thus only certain adaptational characteristics of a plant species, i.e., those found in Begonia, were capable of utilizing this habitat most successfully.

CLUMPING BEHAVIOR: NUMBER OF INDIVIDUALS/CLUMP

Table 4 categorizes the number of clumps in each quadrat, including the percentage of the number of individuals in each clump. Understanding that the data are limited, a trend is observed among A, D and F, and the total percentage of individuals occurring in clumps. As A, D, and F increase, so does the percentage of individuals found in clumps. The plot for A/F does not support or reject a trend with the percentage of individuals occurring in clumps. Quadrats with few individuals exhibit higher percentages of individuals occurring singly; these include quadrats 6, 7, and 3I, six with 69.2% of its individuals occurring singly, seven with 45.2% found singly, and three-one with 45% represented as single individuals.

Quadrat number 5II for B. nelumbiifolia exhibits the greatest diversity in clump size, ranging from 2 to 10 individuals/clump. The population within this plot is considerably greater than the other quadrats also. Comparatively large clumps of 8, 9, and 10 are observed within this quadrat, though only one clump of 8 is observed for B. heracleifolia in quadrat 2 and one clump of 9 for B. californica in quadrat 10. 46.2% of the individuals in quadrat 5II are found in clumps of 8, 9, and 10.

It may be noted that it is not necessarily expected that an increase in A, D, or F would result in an increase of clumping. Besides clumping, other types of spatial development of a plant species are possible: for instance, a more evenly distributed pattern, where single individuals or two or three individuals/M^2 are possible rather than development of larger size clumps exhibited by these species of Begonia. This observed trend regarding the clumping behavior of these species of Begonia may be a direct

TABLE 4

NUMBER OF CLUMPS/QUADRATS AND PER CENT OF INDIVIDUALS

Grid	Clump Size										Total Per Cent
	1	2	3	4	5	6	7	8	9	10	
1	2(3.9)	5(19.6)	4(23.5)	3(23.5)	1(9.8)	2(23.5)	0	0	0	0	99.9
2	7(15.2)	4(17.4)	3(19.6)	2(17.4)	0	0	1(15.2)	1(17.4)	0	0	87.0
3I	9(45.0)	0	1(15.0)	2(40.0)	0	0	0	0	0	0	55.0
3II	8(17.4)	4(17.4)	3(19.6)	1(8.7)	1(10.9)	2(26.0)	0	0	0	0	82.6
4I	5(13.2)	4(21.1)	4(31.6)	2(21.1)	1(13.2)	0	0	0	0	0	87.0
4II	10(28.6)	6(34.3)	3(25.7)	1(11.4)	0	0	0	0	0	0	71.4
5I	8(15.7)	11(43.1)	4(23.5)	1(7.8)	1(9.8)	0	0	0	0	0	84.2
5II	8(5.9)	3(4.4)	10(22.1)	2(5.9)	3(11.0)	1(4.4)	3(17.6)	1(6.6)	3(22.1)	0	94.2
6	9(69.2)	2(30.8)	0	0	0	0	0	0	0	0	30.8
7	14(45.2)	5(32.3)	1(9.7)	1(12.9)	0	0	0	0	0	0	54.9
8	11(22.9)	5(20.8)	4(25.0)	1(8.3)	1(10.4)	1(12.5)	0	0	0	0	77.0
9	9(25.0)	3(16.7)	1(8.3)	1(11.1)	1(13.9)	0	0	0	1(25.0)	0	75.0

FIG 2

Relation of A.D.F. & A/F to % of Individuals Occuring in Clumps

% of Individuals Occuring in Clumps
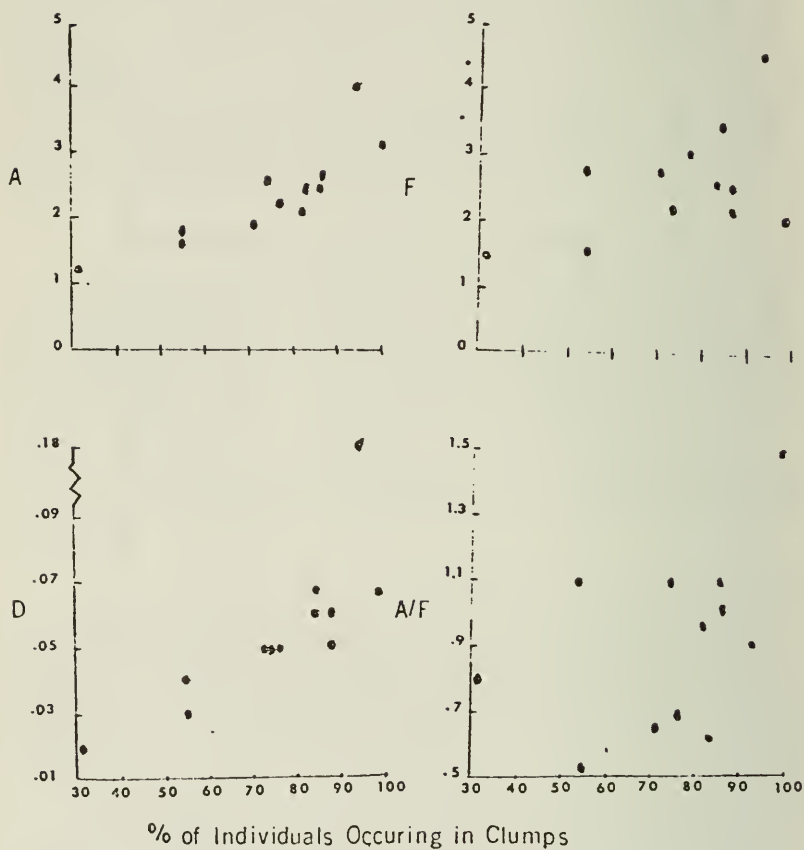
manifestation of the species' reproductive biology.

CLUMPING BEHAVIOR: COMMON BOUNDARY VALUES

Table 5 presents the data on CBV. The region with plants sharing the most common boundaries is quadrat 5, for B. nelumbiifolia. In groups 5A, 5C, and 2D the number of common boundaries exceeds the number of occupied M^2 within the group, indicating maximum clumping behavior for these plots; 5IIA for B. nelumbiifolia has a CBV of 13:18, 5IIC a CBV of 5:6, and 2D for B. heracleifolia has a CBV of 7:12.

B. heracleifolia indicates the highest CBVs of the three species observed in this study, in spite of the very high values for B. nelumbiifolia in quadrat 5II. The next greatest values for common boundaries are observed in groups 5ID, 2A, and 4IC for B. heracleifolia, having, respectively, ratios of 22:14, 8:7 and 9:7. Quadrat 5 thus exhibits the largest CBV for both B. heracleifolia and B. nelumbiifolia.

In quadrat 2 of B. heracleifolia 93.5% of the individuals are found aggregated in two clumps, 2A and 2D. For quadrat 3, B. nelumbiifolia exceeds B. heracleifolia in total number of individuals by 26, or more than 100%, but B. heracleifolia has a CBV of 7:5, for the largest group. In quadrat 4, B. heracleifolia exceeds B. nelumbiifolia by three individuals but exhibits a considerably larger CBV at 9:7, for the largest group. B. californica shows one high CBV of 9:5 in quadrat 8.

Considering the clumping behavior in terms of the different analyses, number of individuals/clump and CBV, suggests some interesting variances, even though the scarcity of the field data negates the validity of statistical tests. B. nelumbiifolia has the greatest number of average individuals per quadrat of the three species, exhibits the largest number of individuals per quadrat, and the largest clumps, while higher CBVs are found for B. heracleifolia more often than the other species. Also, B. heracleifolia has the lowest average number of individuals per quadrat. These data suggest that individuals of B. heracleifolia have a greater tendency to form clumps occupying a larger surface area than B. nelumbiifolia or B. californica.

SYMPATRIC ASSOCIATION

OF B. HERACLEIFOLIA AND B. NELUMBIIFOLIA

B. heracleifolia and B. nelumbiifolia have been reported to occur within the same regional area near Ococoatozula, Chiapas (Ziesenhenne 1947), though the degree of association of the two species was not reported by the original collector. The sympatric association of these species at the Misola waterfall is defined

TABLE 5

COMMON BOUNDARY ANALYSIS

(No. of Occupied M² / Group / No. of Common Boundaries)

Quadrat Number and Species	A	B	C	Group Position D	E	F	G	H	I	J	K
1 B. heracleifolia	2:1	3:2	2:1	4:2	5:2	1:0					
2 B. heracleifolia	8:7	1:0	1:0	7:12							
3I B. heracleifolia	2:0	7:5	2:0	1:0							
3II B. nelumbiifolia	3:2	6:4	4:0		3:2	3:3					
4I B. heracleifolia	1:0	3:2	9:7	2:1	1:0				1:0		
4II B. nelumbiifolia	1:0	1:0	5:2		2:0	4:2	3:2	3:3			
5I B. heracleifolia	1:0			22:14	2:0						
5II B. nelumbiifolia	13:18	3:2	5:6	7:3	5:4						
6 B. heracleifolia	1:0	1:0	4:2	1:0	1:0	1:0	1:0	1:0			
7 B. heracleifolia	1:0	7:6	6:5	1:0	1:0	1:0	1:0	2:0	1:0		
8 B. californica	4:4	1:0	9:5	1:0	1:0	1:0	1:0	1:0	2:1	1:0	1:0
9 B. californica	5:3	2:0	3:0	1:0	2:1	2:0	1:0				

within the limits of three 25 x 30 meter quadrats. The data pre-
sented in Table 5 indicate that B. heracleifolia and B. nelumbii-
folia show closer intra-species spatial orientation than inter-
species spatial orientation. Of the 20 designated groups listed
in Table 6 and represented in Fig. 3, eleven, or 55.0%, are com-
prised of a single species; six groups, or 30.0%, are ones having
a minimum of 75.0% dominance for one species, and the remaining
four groups have between 63.0% and 66.7% dominance. The lowest
percentage of dominance is 63.0% for B. nelumbiifolia found in
quadrat-group 3B. The distribution of individuals within quadrat
3 exhibits the lowest percentages of dominance of the three quad-
rats, for there are more individuals of both species occurring in
close proximity to one another per group than in the other two
25M x 30M quadrats. Fig. 4 is a photograph showing the sympatry
of these species of Begonia.

     Considering that these species occur sympatrically within the
same habitat, the degree to which they are associated is minimal.
Of the 113 individual square meters occupied by B. heracleifolia
and B. nelumbiifolia only 10, or 8.8%, are found to have both spe-
cies within the same square meter.

     The following locations are the only places where B. hera-
cleifolia and B. nelumbiifolia occupy the same square meter: in
quadrat-group 3B there are two occurrences of sympatry, in quadrat
4, four occurrences of sympatry, one in group B, three in group B,
three in group C, and in quadrat 5, one occurrence each in groups
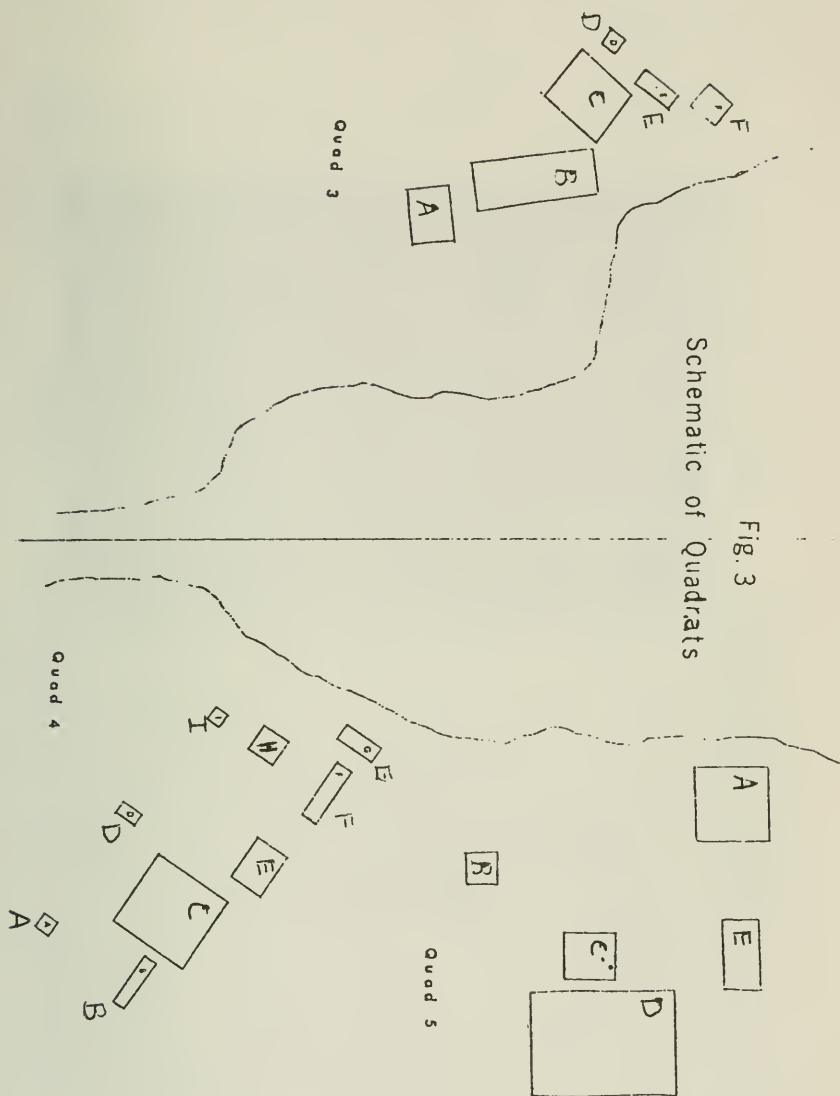A and D, and two occurrences in group E.

     The distinct patterns of segregation exhibited by these
species of Begonia appear to be based on micro-habitat prefer-
ences. B. nelumbiifolia shows a greater preference to the area
near the pool side, while B. heracleifolia shows a preference for
the forest margin. Table 6 lists the approximate distances the
groups are from the margin of the pool. Those groups found closer
to the present margin of the pool are comprised virtually always
of B. nelumbiifolia, while those groups furthest from the pool are
mostly B. heracleifolia. The exception to this is quadrat-groups
3A and 3B, where B. nelumbiifolia is the dominant species, but is
found furthest from the margin. In quadrat-groups 3A and 3B there
is the lowest degree of dominance since both species occur to-
gether at a higher frequency than in the other quadrats.

     B. nelumbiifolia generally has lower percentage ratings for
the dominant species within a group. Several explanations may be
offered: 1. B. nelumbiifolia has a greater range of habitat tol-
erance than B. heracleifolia. 2. The population of B. nelumbii-
folia has been represented at the habitat for a longer period of
time, thus allowing for a wider habitat distribution than B.
heracleifolia. The specific adaptational characteristics of these
species that determine such habitat preferences are not known, but
the rhizome of B. nelumbiifolia is distinctly smaller in diameter

TABLE 6

NUMBER OF INDIVIDUALS IN GROUP WITH PER CENT OF DOMINANCE

AND DISTANCE FROM POOL MARGIN

Quad. No.	Group Position	B. heracleifolia	B. nelumbiifolia	Approximate Distance from Pool Margin (in meters)
3	A	2	7 (77.8%)	6.0
3	B	10	17 (63.0%)	6.9
3	C	4	7 (63.6%)	4.3
3	D	4 (100%)	0	5.6
3	E	0	·9 (100%)	3.5
3	F	0	6 (100%)	2.5
4	A	3 (100%)	0	11.4
4	B	8 (80%)	2	12.0
4	C	24 (75%)	8	9.3
4	D	3 (100%)	0	7.2
4	E	2	4 (66.7%)	6.7
4	F	0	6 (100%)	3.0
4	G	0	4 (100%)	1.5
4	H	0	4 (100%)	2.8
4	I	1 (100%)	0	2.8
5	A	1	84 (98.8%)	2.3
5	B	0	10 (100%)	4.5
5	C	0	16 (100%)	7.5
5	D	47 (82.5%)	10	10.4
5	E	3	15 (83.3%)	7.5

Fig. 3   Schematic of Quadrats

than B. heracleifolia. A smaller rhizome would be less likely
to be uprooted in a torrential flood than a larger one having a
greater surface area exposed to the current.

The position of the quadrats at the Misola waterfall contri-
butes information regarding these species' spatial distribution,
also. Quadrat 3 was set up on the northeast side of the pool.
Quadrat 3 has the fewest total number of individuals of the three
quadrats, 66. Quadrat 4 has 69 individuals and quadrat 5 has the
greatest, with 212 individuals, which is the grid that was set up
parallel and adjacent to the cliff wall. In quadrat 5 are found
45.3% of the total individuals of B. heracleifolia and 63.2% of
B. nelumbiifolia. B. nelumbiifolia is heavily populating the
cliff face; thus it would appear that seed has been dispersed
from plants on the cliff to the area below, implying that the
cliff region was occupied prior in time to the region surrounding
the pool. At least the likelihood of seed being dispersed down-
ward is greater than dispersal upward. B. heracleifolia was not
observed to inhabit the cliff area at all. The smaller rhizomes
of B. nelumbiifolia may also offer some explanation for this
occupying the cliff face and not B. heracleifolia.

DISCUSSION

The differences in A, D, and F values for the southern and
the northern regional populations of B. heracleifolia are worth
noting. Specimens of B. heracleifolia from the Gray Herbarium in-
dicate this species has been collected twice in Nayarit, and once
in Hidalgo, being the next northernmost collections. This suggests
a more limited northern population size than the abundantly repre-
sented material from southern Mexico and Guatemala. The limited
number of northern collections of this species suggests that these
populations are on the periphery of the range of B. heracleifolia,
and likely make up the northern species border. It is well known
that isolated populations and morphological variation occur on the
perphery of a species range (Grant 1971, Mayr 1963). B. heraclei-
folia is reported to have four varieties according to Barkley and
Golding's (1972) list, which indicates the species is quite vari-
able in morphology. The morphological variation of the population
of B. heracleifolia observed in the Sinaloa population may event-
ually warrant being described as another variety. Distinct dif-
ferences are noted in the flower size, bract shape being larger
and more persistent, and leaf lobes less indented, to name several
variations. Frequently morphological variation is clinal (Mayr
1963, Endler, 1977), where certain specific character traits vary
along a gradient. The possibility cannot be discarded that B.
heracleifolia exhibits clinal variation, though several character-
istics will have to be measured in order to determine this.

The example of an isolated population is that of B. califor-
nica of Baja California. Only several collections have been made

Fig. 4 - Example of
Sympatric Association of
B. heracleifolia (star shaped
species under palm on left)
and B. nelumbiifolia (palmate
species to the right) growing
near forest margin.

of this species: two on Baja California Sur (Carter personal communication), one in Sonora, Mexico, one in Nayarit, Mexico, and several collections from Sinaloa, and the Tres Marias Islands (Ziesenhenne personal communication). Like many species in the Begoniaceae, B. californica would be considered a rare species, thus data collected on spatial distribution is at no great loss for the species itself has a limited population size.

Spatial distribution patterns of these species of Begonia indicate a distinct tendency to clump, for the plants do not exhibit an evenly distributed pattern. This clumping behavior may be explained in several ways: 1) poor seed dispersal, 2) vegetative reproduction, 3) micro-habitat variances, such as moisture availability.

Other works on spatial patterning of tropical plants include the works of Ashton (1969) and Poore (1968), both of whom report on patterning of trees, whose reproductive biology is completely different from that of the herbaceous Begonia. Ashton (1969) points out that clumping is observed in families which have poor dispersal mechanisms, with specific reference to Shorea polyandra of the Dipterocarpaceae in W. Sarawak, Borneo. Though the Dipterocarpaceae are a tropical tree family, Ashton explains that the clumping is caused by poor seed dispersal as compared to wind dispersal of seed in families like Apocynaceae and certain Leguminosae (Koompassia). Poore (1968) also has shown that contiguous distribution is common among tropical rainforest trees. Even though the differences between herbs and trees is considerable, one cannot discount the possibility that clumping in the Begoniaceae may be attributed to poor seed dispersal. Once an individual becomes established and flowers, seed is dispersed within a short distance of the parent plant. Because the Begoniaceae show preferences to stream margin habitats there is a good possibility that water dispersal is a mechanism for local dispersal of seed. Within a regional area water dispersal could be a very efficient mechanism for establishing a population. On many occasions I have observed seedlings growing right next to the flowing water, often lodged in small cracks in rocks or spaces between exposed roots. Also, one may observe a large population of a species upstream and a single plant or a small population downstream.

The other possible means by which clumps could be developed is through vegetative reproduction in which case "clone" may be the more appropriate term to describe the pattern. The author has observed individuals of the Begonia media Merr. & Perr (affinity) complex in Papua New Guinea frequently give rise to separate individuals by vegetative means. A stem will bend over until it touches the ground, root at the nodes, and a subsequent decay to the first several internodes of the branch occurs, leaving a separate individual. The same situation has been observed by Art (personal communication) for Phragmites communis on Fire Island, New York. Specific work on the mechanisms of vegetative repro-

duction in _Medeola virginiana_ has been reported by Bell (1974),
who shows how a parent plant will produce rhizomes in varying
directions, each of which results in a separate individual.
Holler and Abrahamson (1977) have experimentally shown that vege-
tative "reproductive effort" is higher in low density plots for
Fragaria virginiana of the Rosaceae, and that seed "reproductive
effort" is unaffected by plant density. In the case of rhizo-
matous species of _Begonia_, vegetative reproduction could occur by
a mechanism similar to that observed in _B. media_, or the above-
mentioned other species, since separate individuals were observed
and counted. The rhizomes on these plants are found above the
ground, while in other species the rhizome is below the ground,
which makes it extremely difficult to distinguish separate indi-
viduals. It may be noted again that one can observe separate in-
dividuals within a clump of _Begonia_, but the genetic character of
the clump poses an interesting idea, since vegetative reproduction
results in individuals having identical genomes. In the event of
vegetative reproduction being the principal mechanism for clump
development, the possibility exists for defining the entire clump
as the individual. I consider the autonomy of the organism as the
greater priority, and would thus continue to utilize the definition
adopted in this paper.

    Grant (1971) utilizes the term _evolutionary potential_ (a term
having considerable meaning from a metaphysical standpoint) when
describing clonal complexes, stating that species exhibiting such
complexes have a simpler taxonomic structure than agamic groups.
The taxonomy of the Begoniaceae is very complex (Schubert, per-
sonal communication) and sexual reproduction is definitely in-
volved in the development of clumps, because seedlings can be ob-
served. Thus, if asexual reproduction is involved in _B. hera-
cleifolia_ and _B. nelumbiifolia_, they would more likely be consid-
ered agamic complexes than clonal.

    The presence of residual meristematic potential, particularly
in the section Gireoudia, to which _B. heracleifolia_ and _B. nelum-
biifolia_ are assigned, raises the question concerning the function
of a residual meristem. The residual meristem of _Begonia_ allows
horticulturists to vegetatively propagate leaf cuttings, as men-
tioned by Howard (1974). It is speculative whether there is any
significance between this residual meristematic potential and the
possibility of asexual reproduction in _Begonia_. Possibly the re-
sidual meristem is a characteristic that had adaptive significance
at some earlier point in the evolutionary history of _Begonia_, and
subsequently the trait was selected against. The frequency of a
residual meristem is very limited in flowering plants, occurring
in such families as Piperaceae, Gesneriaceae, Crassulaceae, and
Cactaceae, the first two families listed having genera that often
are associated with _Begonia_ along the stream margins of the trop-
ics, also. The questions regarding the ability of _Begonia_ to re-
produce vegetatively are of interest and will involve considerable

research, both in the field and in the laboratory.

The sympatric occurrence of B. heracleifolia and B. nelum-
biifolia shows some very interesting patterns. The environment
in which the two species grow appears to be subject to flooding.
The large pile of logs at the periphery of the pool area would
indicate that during the wet season, when heavy rains occurred,
trees would be uprooted and tend to accumulate at the base of the
waterfall. The orientation of B. heracleifolia and B. nelumbii-
folia around the margin of the pool indicates habitat preferences.
B. heracleifolia shows a very high frequency of occupation further
from the pool, whereas B. nelumbiifolia has a degree of preference
close to the pool, although it frequents the forest margin as well.
The spatial distribution patterns of each species at this location
is different also, since B. heracleifolia shows greater CBVs than
B. nelumbiifolia. B. nelumbiifolia is much more evenly distribu-
ted within this habitat than B. heracleifolia. The larger CBVs
of B. heracleifolia indicate that individuals become established
in clumps which are more spread out than in B. nelumbiifolia, in-
dividuals of this species being aggregated in smaller groups with
greater distance between the groups. Ashton (1969) mentions that
within the interspecific competition between species, evolution
tends toward the mutual avoidance of the species, thus allowing
for greater population densities of the species. In the case of
the sympatry of B. heracleifolia and B. nelumbiifolia mutual
avoidance has been established since the patterns of dominance in-
dicate high percentages of individuals of one species or the other
within the observed groups of the quadrats.

No hybridization was observed among B. heracleifolia and B.
nelumbiifolia, even though they occurred in a mixed population.
The question is why no hybridization occurs between the two spe-
cies, particularly when they have been reported to hybridize in
cultivation. Thompson (1976) lists the parentage of a cultivar
named "B. Lettonica" as B. heracleifolia X B. nelumbiifolia.
Several points may contribute to explaining this dichotomy. 1)
The original parentage was not identified correctly, thus making
"B. Lettonica's" ancestry different from that suggested. 2) At
other geographical locations the genetic structure of one species
may be significantly different to allow hybridization to occur.
Perhaps one of the varieties of B. heracleifolia was used. 3) In
the course of time, a cultivated species, being frequently prop-
agated, may assume certain variations which are not found in the
wild.

Within the section Gireoudia, to which approximately 60 spe-
cies are reported (Barkley and Golding 1974), there is known to be
considerable hybridization (Thompson 1976). According to the
specimens in the Gray Herbarium, most species within Gireoudia
have much more restricted geographical distributions than B. hera-
cleifolia and B. nelumbiifolia. It is curious as to why no hybrids
were observed between B. heracleifolia and B. nelumbiifolia at the

Misola waterfall, when many species of Gireoudia show a frequent
ability to hybridize. What factors contribute to this inability
to hybridize in the wild? A great deal of literature is available
to explain barriers to hybridization between closely related plant
species. In the sympatric association of Cercidium floridum and
C. microphyllum in California, ultraviolet floral patterns are
suggested as a pre-pollination isolating mechanism (Jones 1978).
The lack of hybridization between B. heracleifolia and B. nelum-
biifolia may involve differences in pollinators themselves, which
has been reported to occur in Salvia (Grant and Grant 1964).
Mechanical barriers leading to a maintenance of a species' char-
acteristics may involve morphological differences. Pollen grains
of B. heracleifolia and B. nelumbiifolia were compared under a
compound microscope, the former species having pollen nearly twice
as large as the latter, which may have something to do with the
inability of these species to hybridize.

The spatial distribution patterns revealed by these species
of Begonia are of interest, for it is not necessarily expected
that as the number of individuals within a quadrat increases, the
percentage of plants occurring in clumps increases. The tendency
of these Begonias to form clumps is a characteristic feature among
many species within the genus. The many factors which may contri-
bute to this type of spatial distribution are not known, but the
fact that Begonia has a preference for stream margins may have a
bearing on their spatial distribution patterns.

The antiquity of the stream margin habitat of the tropics has
been mentioned by Regel (1977) and is considerable interest since
this habitat is continually subject to disturbance. The periodic
inundation of torrential water flowing down a stream bed would
frequently remove the vegetation growing along the margin of the
stream. When hiking stream beds in the tropics, one can observe
the same plant taxa associated with the stream margin on numerous
occasions. Species of Cytrandra, Impatiens, Pilea, Piper, Rosa,
and Urtica (genera of the Melastomataceae and Zingiberaceae), are
frequently associated with Begonia along the stream margins. This
is not to say that the above-mentioned taxa are restricted to
stream margins, any more than Begonia, but there appears to be a
high frequency of observing the same taxa on many occasions; it is
like many other habitats, in that certain species, or taxa, are
found associated with particular habitats, as shown by El-Ghonemy
et al. (1977). Since this habitat of the tropics is so susceptible
to disturbance, the question arises of how long these taxa, and
many others, have inhabited these particular environments. One
wonders whether these herbaceous angiosperms always have occupied
the disturbed stream margin environments or whether there has been
a great variety of different taxa that have come and gone within
the habitat.

Graham (1975) points out that the tropical lowland rain
forest in Vera Cruz, Mexico has experienced substantial floristic

change since the upper Miocene, contrary to the widely held view that the tropical rain forest has remained relatively unchanged for the last several million years (Dobzhansky 1950, Ashton 1969). The possibility exists that the stream margin habitat of the tropical rain forest represents a place of rapid floristic change and speciation. The fact that the climatological conditions of the tropical rain forest contribute to the great diversity of species generally may have a bearing on the variability of species that occupy the specific stream margin habitats.

It is curious to note the tremendous variability within certain species of _Begonia_, and for that matter within the entire genus. Certain species such as _B_. _heracleifolia_, _B_. _lindleyana_ Walp., _B_. _media_, _B_. _micranthera_ Gris., _B_. _simulans_ Merr. and Perry, _B_. _stigmosa_ Lindl., or _B_. _urtica_ L.f. show great morphological variation, in some cases characterized by several varieties in a species, and in others the complexity is so great that every regional collection, represented by a herbarium specimen, may be treated as a different taxon. It is possible that the notable variability of _Begonia_ is influenced by the habitats which species occupy. The genetic system of _Begonia_ could be modified in response to the disturbance found at the stream margin habitat of the tropical rain forest; this idea may be applicable particularly to _Begonia_ and, of course, certain other genera, because the genus shows variation that is greater than many other angiosperm genera. The above speculations have no basis as yet for any interpretation, as do the minimal data of this paper, but the curiosity arising when one is collecting in the tropical rain forest will forever remain a pleasure, as anyone who works there has experienced. Such speculations serve as possible guidelines for future work on the Begoniaceae and expose aspects of the group which are of botanical interest as a whole.

ACKNOWLEDGMENTS

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